

OBSERVATIONS ON THE POSSIBLE USE OF HABITAT CUES AND TOKEN STIMULI
BY CATERPILLAR-HUNTING WASPS: *EUODYNERUS FORAMINATUS*
(HYMENOPTERA, EUMENIDAE)

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Quaestiones Entomologicae
20: 25-33 1984

ABSTRACT

Observations in the wild and a few tests in captivity gave indications that host-finding by the caterpillar-hunting eumenine wasp Euodynerus foraminatus depended mainly on two categories of stimuli: a) habitat cues such as green vegetation, leaves of trees, shrubs and plants, which were readily detected and investigated in captivity, even in the absence of prey or prey-related stimuli. The interest for such stimuli was short-lived, however, and they had no activating effects on the wasps. b) Token stimuli provided by the leaf-rolling microlepidopteran prey such as rolled leaves, frass, silk or odor left on leaves, produced longer lasting and activating effects. Upon contact with the antennae the wasps became very excited, chewed the stimuli and ran around wildly. Only the prey itself was stung, however. Parasitic Hymenoptera such as wood wasps (Siricidae), which hunt well concealed prey, also use habitat cues and/or token stimuli for host-finding. Some sphecid wasps that attack highly mobile and exposed prey such as common grasshoppers apparently do not use such cues.

RÉSUMÉ

Des observations sur le terrain et quelques tests de laboratoire semblent indiquer que certaines guêpes telles qu'Euodynerus foraminatus (Eumenidae) utilisent deux types de stimuli durant la chasse de leurs proies, des larves de Microlepidoptères qui vivent entre plusieurs feuilles enroulées: a) des stimuli reliés à l'habitat, par exemple des feuilles d'arbre, d'arbustes ou de plantes, qui sont visitées en captivité même en l'absence de proies ou de stimuli produits par ces dernières. Cependant l'intérêt suscité par de tels stimuli n'est que de très courte durée et aucun effet activateur n'est produit. b) Des stimuli-substituts de la proie tels que des feuilles enroulées, des excréments, fils de soie ou odeurs, laissés sur les feuilles par la proie suscitent un intérêt durable et produisent une vive excitation lorsque les antennes de la guêpe entrent en contact avec eux. La guêpe peut même mordre de tels objets mais elle ne piquera que la proie elle-même. Des guêpes parasites telles que les Siricidae, qui chassent des proies cachées, utilisent également des stimuli-substituts ou reliés à l'habitat. Ce n'est apparemment pas le cas pour des Sphégides qui s'attaquent à des proies très mobiles et exposées, telles que des criquets communs.

INTRODUCTION

Some mammal-infesting ticks drop to the ground upon detection of butyric acid. Some leeches find their warm-blooded hosts on the basis of an increase in local temperature. Similarly, various parasitic Hymenoptera, such as braconid, ichneumonid or siricid wasps also use such "token" stimuli for host-finding or host-detection, for instance frass, symbiotic fungi or gland secretions left during oviposition by the host species, or even heat cues (see for instance Heatwole *et al.* 1963, 1964; Spradbery 1968, 1970; and Richerson and Borden 1972a, b). Habitat cues are even more important for some taxa, particularly when the parasite uses a

variety of hosts all found in the same habitat, shoots of conifers for instance (Townes 1960).

Some aculeate wasps that hunt concealed prey might also use habitat cues and/or token stimuli as the present study suggests.

MATERIAL AND METHODS

Euodynerus foraminatus (Sauss.) was studied as part of a comparative work on prey-stinging methods (Steiner 1983).

Numerous field observations were made on this and other species of eumenine wasps in central Oregon, U.S.A., near Bend (Deschutes Co.) and Cove Palisades (Jefferson Co.) during the spring and summer of 1977. Marking of individual wasps was not very successful, presumably because the population under study was too large and the probability of sighting marked individuals repeatedly, very low. Consequently only general trends were studied, on a qualitative basis.

Individually marked wasps were then studied in cages about 50 x 80 x 50 cm (general methods described in Steiner 1965) and tested with various separate and combined stimuli. Unfortunately among the few that survived only one wasp (No. 1031), caught near Lower Bridge on June 2, came into reproductive condition and responded positively to the appropriate stimuli. No striking individual or species differences were recorded during the field observations. It is therefore felt that data gathered on this single individual are probably representative of the species. Previous studies of various wasps in captivity (from 1952 on) have also shown that prey-related activities are generally very stereotyped.

The stimuli used singly or in combination were: a) the prey itself, namely various unidentified leaf-rolling microlepidopteran larvae commonly found on trees or shrubs such as *Salix* spp., *Populus* sp., and also a few suitable leaf-rolling larvae of unidentified sawflies, also accepted by the wasp which is not very prey-specific; b) token stimuli produced by the prey, such as rolled leaves and/or the silk used to hold these leaves together, leaves rubbed on the prey or on frass (odor of prey); c) isolated leaves of various trees, shrubs or plants (mostly *Salix* spp.) taken from non-infested small shrubs or branches isolated from possible contacts by fine gauze wrapped around them. Complete absence of prey-related stimuli was confirmed later, on the basis of lack of any activating effects on the wasp (see results), whereas prey-related stimuli (silk, frass, etc.) invariably produced striking effects, described later, when the wasp was in hunting condition. To avoid contamination of the cage, stimuli were placed on pieces of aluminum foil removed after each trial. After stinging, the prey was also immediately removed from the cage before the wasp could carry them in the cage and disseminate the odor by contact.

In order to avoid or minimize conditioning of the wasp, patterning of the conditions of presentation was carefully avoided by varying widely and arbitrarily the time, order and location of presentation as well as the kind of stimulus situation. The stimuli were introduced in the cage very slowly, through a small lateral door in order to avoid sudden movement or mechanical disturbances that could have provided signals to the wasp. Leaves without prey or token stimuli and pieces of aluminum foil were also left routinely in the cage for extended periods of time in order to break any strong association of such objects with the reward of a prey (positive reinforcer).

RESULTS AND DISCUSSION

Field observations

The major aim was to get some general idea about the methods of host-finding used by various eumenine wasps and females of *E. foraminatus* in particular. Such wasps were found in large numbers on various trees and shrubs, particularly *Salix* spp., *Populus* sp., *Alnus* sp., etc. along the banks of the Deschutes River. All eumenid wasps observed proceeded essentially in the same way. They inspected summarily (I in Table 1) a large number of individual leaves and after a while flew to another area of the same or a different tree. The pattern of searching changed drastically as they found rolled leaves, groups of leaves held together with silk (Fig. 1A), leaves covered with silk (Fig. 1B) or with frass. Such token stimuli were carefully investigated (SI in Table 1) with the antennae (Fig. 1B) and had clearly a special significance for the wasps. The latter became very agitated (activation=A in Table 1) and often started chewing vigorously the leaves or silk (CH in Table 1; Fig. 1A). The wasps intensified their search which also became much more localized. Their movements became very jerky and were oriented in many different directions. The wings were open and spread apart and the mandibles open, apparently in preparation for pouncing on a prey organism. If presence of a prey organism inside the rolled leaves was confirmed by antennal inspection, wasps then intensified their attack with the mandibles and chips of vegetation were detached from the base of the leaves (Fig. 1A) and the resulting hole was progressively enlarged. This hole and/or the open extremities of the rolled leaves were also frequently inspected and the wasps also poked their abdomen tip into them, in an apparent effort to deliver one or several sting(s), haphazardly, to the invisible prey (= irregular stings: Steiner 1983). Some prey organisms dropped to the ground very suddenly or remained suspended at the end of a thread of silk. Presented with this circumstance, many wasps remained on the vacated leaves, apparently activated by the still present odor of the prey. At other times the wasps were successful in extracting the prey and immediately undertook to sting them into paralysis with one, two or more stings in the cephalo-thoracic region (details in Steiner 1983: regular stings; see also Fig. 1C). *E. foraminatus* females exhibit little prey-specificity but take only rather small, frail caterpillars such as those of Gelechiidae, Oecophoridae, Olethreutidae, Tortricidae, Pyraustinae, Pyralidinae, etc. (Krombein *et al.* 1979, p. 1495). A few leaf-rolling larvae of sawflies were also accepted. The same lack of strict specificity also appears to hold for the vegetation visited by such wasps.

Study in captivity

Control of variables of the stimulus situation, however imperfect, is possible only under laboratory conditions. In particular, presence of prey-odor on the leaves investigated in the wild could not be ruled out. The results of 53 trials with various stimulus situations are summarized in Table 1. Interpretation of the results requires some preliminary comments. First, such experiments should involve independent samples, but the number of wasps required would have been prohibitive because they are difficult to raise, and in fact only one wasp survived. Second, the measured durations (cols. 3 and 4) are highly variable or were not determined (priority was given to stinging patterns). Therefore, for these various reasons, a statistical analysis would not be meaningful. Furthermore, probability of detection of the stimuli presented does not remain constant over time since it depends among other things on: 1) the internal state of the wasp, which fluctuates over time, both on a short- and long- term basis; 2) location of the wasp relative to that of the stimulus situation presented also varied considerably; 3) the general level

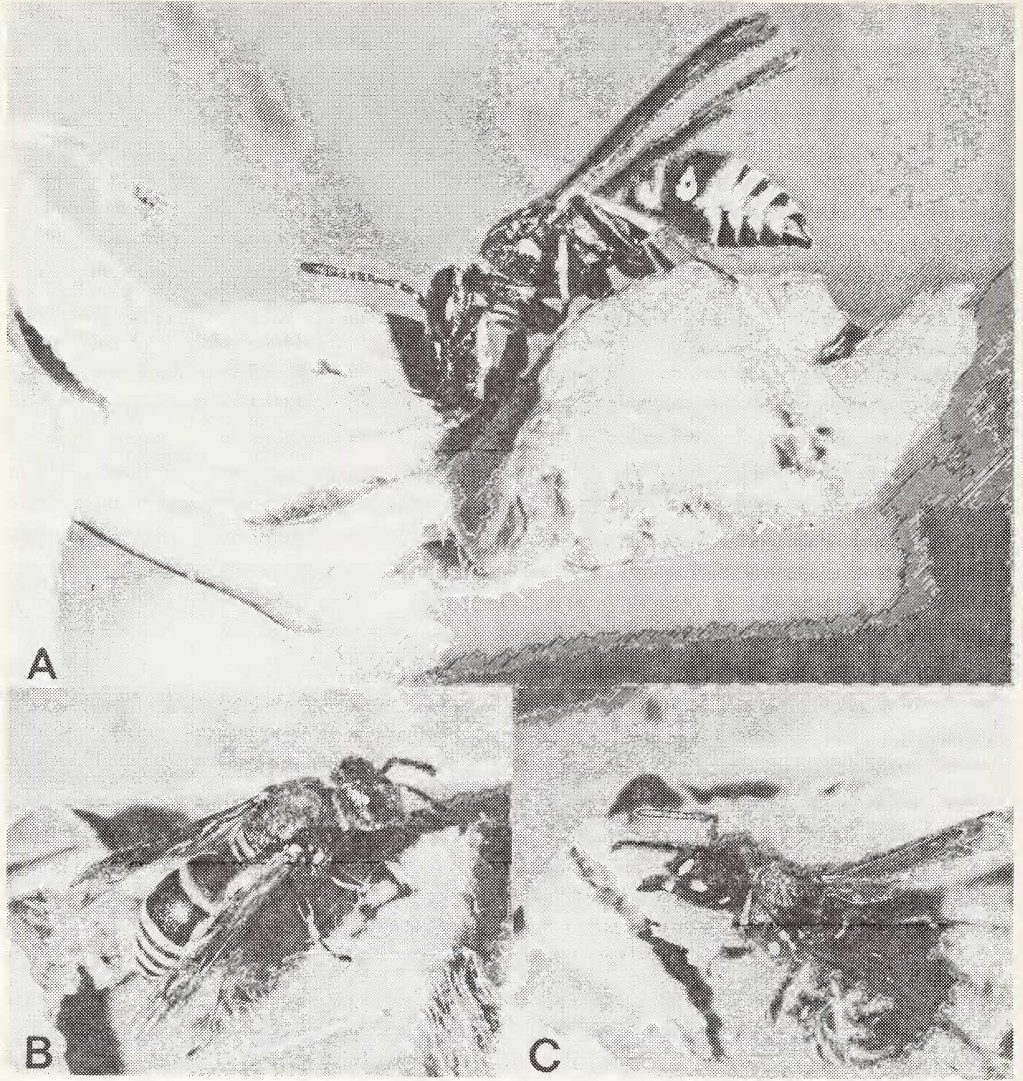


Fig. 1. *Euodynerus foraminatus* wasp carefully investigating (A) a group of leaves held together by silk threads spun by a larva of Microlepidoptera or Tenthredinidae; the wasp starts attacking the base of the shelter with her mandibles; (B) silk threads covering a *Salix* leaf are probed with the antennae and then chewed with the mandibles; (C) after extraction of the caterpillar from its shelter, the wasp stings the prey into paralysis.

Table 1. Results of 53 trials (tests) with various stimulus situations presented to wasp No 1031 (*Euodynerus foraminatus*) in captivity. List of abbreviations: *col.2*: L=leaves (in parenthesis: S=*Salix* spp., P=*Populus* sp., V=*Verbascum [thapsus?]*, P=*Plantago* sp., L=lettuce, G=green grasshopper, ?=non-identified); P=prey (various suitable larvae of microlepidopterans, mostly leaf-rollers; a few tenthredinid larvae); T=token stimuli (in parenthesis: R=rolled leaves, S=silk threads on leaf, O=odor on leaf) - *Cols 3 & 4*: m=minutes; s=seconds (if preceded by f, means a few minutes or seconds); X: visit of undetermined duration, preceded by number indicating number of visits; successive visits separated by commas - *Col.5*: I=short investigation; SI=sustained (careful) inspection; A=activation effects ("arousal"); CH=chewing excitedly the vegetation and/or token stimuli; ST=stinging of prey (number in parenthesis refers to diagram showing stinging pattern in Fig. 3 of Steiner, 1983).

1		2	3	4	5	
Presentation time		Stimulus situation	Latency of discovery	Duration of interaction(s)	Effect(s) on wasp	
Month	Day	Hour				
Jn	19	1310	L(?) + T(R) + P	fs	m:7,5	SI, A, CH
		1324	id	fs	m:3, 1-2?, 1-2?, X, 13, 3X	SI, A, CH
		1440	id	fs	X, 2X	I
		1515	P	fs	m:10	SI, A, ST
	20	1321	P	not found	/	/
		1325	P	id	/	/
		1331	P	id	/	/
	30	1400	L(V)	m:64	X (short)	I
		1545	id	m:19	id	I
Jl	5	1105	L(S) + P	not found	/	/
		?	L(S) + T(S)	?	m:20+, 2X	SI, A, CH
		1515	L(S) + T(S+O)	fs	?	SI, A
		1528	L(S) + T(S) + P	fs	?	SI, A, ST(1)
	6	1110	L(S) + P	m:50	fs	I(preay not found)
		?	L(S) + P	?	fm	SI, A, ST(2)
	7	1140	L(S) + P	m:3	fm	I(preay not found)
		?	L(S) + P	?	fm	SI, A, ST(3)
	10	1121	L(S) + P	m:9	fm	SI, A, ST(4)
		1220	id	fs	fm	SI, A, ST(9)
		1242	id	m:15	fm	SI, A, ST(13)
		?	L(S)	?	fs, X (short)	I, I

(continued on next page)

Table 1 (continued)

1 Presentation time MonthDay Hour		2 Stimulus situation	3 Latency of discovery	4 Duration of interaction(s)	5 Effect(s) on wasp
	1352	L(P) + P	m:8	fm	SI, A, ST(18)
11	1200	L(S) + T(S)	fs	X, X, X...? (short)	I, SI, A, CH
	1207	L(S) + T(S) + P	m:3	fm	I, SI, A, ST(10)
	?	L(S)	?	X, X... (short)	I, I...
	1245	L(S) + P	m:3	2X, X (short)	I, I, I
	1300	id	m:5	fm	SI, A, ST(14)
	?	L(S) + T(S)	?	2X	SI, A, CH, I
	?	L(S) + P	?	?	SI, A, ST(19)
	1423	P	m:2	fm	SI, A, ST(5)
12	?	L(L)	?	fs	I
	1328	P	m:2	m:10	SI, A, ST(20)
	1340	L(P)	not found	/	/
	1608	P	m:20	fm	SI, A, ST(15)
	1656	P	m:3	fm	SI, A, ST(11)
	1707	P	m:8	fm	SI, A, ST(6)
13	1800	L(S)	fs	fs	I
	1803	L(S) + P	m:4	m:3	SI, A, ST(12)
	1815	id	m:3	fm	SI, A, ST(7)
	1825	id	m:3	fm	SI, A, ST(16)
	1836	id	m:1	fm	SI, A, ST(21)
14	1330	L(S)	fs	X (very short)	I
	1333	L(S) + P	fs	fm	SI, A, ST(8)
	?	L(S)	?	X (very short)	I
	?	L(S)	?	id	I
	1540	L(S) + P	fs	fm	SI, A, ST(17)
	?	L(S)	?	X (very short)	I
19	1040	L(V)	?	X, X, X... (short)	I, I, I...
	1616	G	?	X, X... (short)	I, I...
28	1130	L(S) + T(S) + P	fs	fm	SI, A, CH, ST(22)
29	1543	L(S) + P	m:4	fm	SI, A, ST(23)
30	1158	L(S)	fs	X(short)	I
	1210	L(S) + P	?	fm	SI, A, ST

of exploratory activity of the wasp was also very variable and could not be controlled or quantified. Effects on the wasp (col. 5) were very clear cut, however, which will therefore be

emphasized.

Results of the tests suggest the following. 1) Most latencies of discovery (col. 3) were short or even very short (a few minutes or seconds); this indicates that the wasp under hunting conditions was very attentive to presence and absence of relevant stimuli in the environment. 2) Leaves devoid of prey or prey-related stimuli (L situation in col. 2) were readily discovered and investigated, but only summarily (I in col. 5) and they did not produce detectable activating effects on the wasp (A in col. 5). Therefore, detection and investigation do not depend on presence of token stimuli and vegetation represents only a habitat cue, presumably detected on the basis of color (green). Incidental observations also point to the probable importance of color: first, on July 19 the wasp investigated a rather large green acridine (slanted-faced) grasshopper, among many brownish oedipodine grasshoppers, that were ignored (grasshoppers were given as prey to *Prionyx parkeri* wasps, also present in the same cage); second, the wasp once escaped from the cage into the field trailer used as "mobile laboratory" and after flying in various directions finally landed on the only green object, an old dried up leaf of *Salix*, discarded from previous trials. In natural conditions, shape of plants, shrubs and trees probably provides additional cues, detected at greater distances. Reactions to color should be systematically investigated, however, and dissociated from shape and vegetation. 3) The low specificity of the vegetation investigated, noticed in the wild, is fully confirmed by tests which included even leaves of lettuce, a plant not associated with suitable prey or token stimuli. Therefore cues such as green vegetation and/or other habitat cues contribute to focus the search of these wasps. 4) In sharp contrast, "token" stimuli (T, col 2) such as rolled leaves [(R), col. 2], odor left on leaves [(O), col. 2], and silk [(S), col. 2] had much more specific, selective, effects (situations L+T, L+T+P, col. 2). They were extensively inspected with the antennae (SI, col. 5) and produced clear activating effects (A, col. 5) on the wasp, including chewing (CH, col. 5) that was not observed with leaves devoid of prey-related stimuli. 5) Only the prey itself, a still more specific stimulus, elicited stinging (ST, col. 5) (cutworm-hunting *Podalonia luctosa* sphecid wasps, tested with single small leaves of dandelion rubbed with cutworm frass, occasionally attempted to sting such leaves, after having assumed the appropriate stinging posture). 6) Only certain areas of the body of the prey receive regular stings (details in Steiner 1983); therefore these various stimuli are organized into a hierarchy involved in increasingly selective responses of the wasp, namely: habitat cues < token stimuli < suitable prey < suitable stinging sites on prey.

Finally, the question of whether habitat cues (vegetation) and/or token stimuli (silk, frass, rolled leaves, odor left on vegetation) are recognized innately or on the basis of their association with the prey (by imprinting or by conditioning) remains open. To solve this problem one would have to use naive wasps that had never been in contact with a prey before. Conditioning was discouraged, however, by withholding the reward of a prey (=positive reinforcer) for extensive periods of time in the cage ("unlearning").

CONCLUSION

Eumenine wasps that hunt hidden prey such as larvae of leaf-rolling Microlepidoptera have evolved a host-finding strategy which is very similar to that used by some parasitic wasps such as wood wasps (Siricidae). It is based on the use of habitat cues and/or token stimuli left behind by the prey. Predictability and reliability of prey-habitat associations appear crucial however. Thus females of the sphecid wasp species *Prionyx parkeri*, studied in the wild in

southeastern Arizona, hunt euryphagous oedipodine grasshoppers which are highly mobile and exposed, and not restricted to any special microhabitat. Consequently the hunting wasps run haphazardly over the ground until they find a prey specimen, without appearing to use any habitat cue or token stimuli to focus their search (Steiner 1981a, b). On the other hand such prey are usually very abundant and the probability of chance encounters very high. In contrast *Podalonia valida* wasps, studied in the same habitat, hunt predominantly or exclusively the much less common lepidopterous larvae of the arctiid ("woolly bears") and systematically inspect plants such as horsemint (*Monarda pectinata*), goldweed (*Verbesina encelioides*) and various "sunflower-like" plants where such prey were usually found (Steiner 1974, 1975). *Prionyx* wasps also visit such plants but only for feeding, resting or sleeping, not during hunting. Previous studies in captivity of numerous sphecid and other eumenine wasps (from 1952 on) have shown that some other wasps such as caterpillar hunters (*Podalonia luctosa*, *Ammophila azteca*, etc.), aphid hunters (*Pemphredon* spp.), various gorytine wasps that hunt leaf hoppers (also *Mimesa* sp.), and curculionid hunters such as *Cerceris* spp. also pay much attention to any vegetation introduced in the cage, while they are hunting. Detailed comparisons among species will be presented elsewhere, along with information on other wasps that hunt hidden prey or prey with restricted habitats or feeding habits.

In summary it is clear that host-finding based on habitat cues and/or token stimuli left behind by the prey is found mostly or exclusively in species that hunt hidden prey or prey species that live in very selective, predictable, habitats. This strategy evolved independently and convergently in wasps as diverse as Ichneumonidae, Siricidae, Braconidae, Eumenidae and Sphecidae.

ACKNOWLEDGEMENTS

The wasp material was kindly identified by R.M. Bohart, Department of Entomology, University of California, Davis, U.S.A. I would like to thank R. Longair for long discussions on the present topic. Research was supported by a grant from the NRCC (No A3499) and funds from the University of Alberta.

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